

A PHYLOGENETIC STUDY OF THE POSTERIOR
METATHORACIC AND BASAL ABDOMINAL
STRUCTURES OF INSECTS, WITH PARTIC-
ULAR REFERENCE TO THE HOLO-
METABOLA

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In order to test the evidence of the relationships of insects, from as widely divergent sources as possible, such markedly different and widely separated structures as the maxillæ, the neck and prothoracic sclerites, and the terminal abdominal structures of female insects, have been compared throughout all of the orders of living insects (see Crampton, 1923, 1926 and 1929); and to the evidence from these sources may be added that furnished by the study of yet another portion of the body, namely, the posterior metathoracic and basal abdominal regions.

Of the lower insects studied, only the blattids, Isoptera, Dermaptera, leaping Orthoptera (*Rhipipteryx*) and psocids (*Zorotypus*) have been included at this time, since it would require too many plates to figure all of the lower types, in addition to the five plates of figures of the Holometabolous forms here described! The discussion of the other lower pterygotan and apterygotan insects will be taken up in another paper dealing with the more important representatives of these insects.

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In discussing the interrelationships of the Holometabola, we may begin with the consideration of the fleas, or Siphonaptera, since the systematic position of these insects is still a matter of dispute, and such evidence as I have been able to gather indicates quite definitely that the fleas could not possibly be derived

from either the Diptera or the Coleoptera, which are the two groups suggested as the precursors of the fleas by most recent investigators. On page 487 of the JOURNAL OF THE NEW YORK ENTOMOLOGICAL SOCIETY, Vol. XXXVII, for 1929, I have summarized the evidence indicating that fleas could not be derived from Diptera or Coleoptera—for the following reasons. The labial palpi of fleas are frequently composed of at least three segments, while the labial palpi of Diptera (labella) and Mecoptera are never composed of more than two segments, and therefore could not serve as the prototypes of the labial palpi of fleas. The metathorax and mesothorax are subequal in fleas, and this condition could not be derived from the dipterous one in which the metathorax is strikingly smaller than the mesothorax (the metathorax of a typical diptron is only a fraction of the size of the mesothorax). The metathoracic coxa is divided into a eucoxa (anterior region) and meron (posterior region) in fleas, and this condition could not be derived from that exhibited by the Diptera, which have no meron in the metathoracic leg.

The mesothoracic and metathoracic coxæ are divided into a eucoxa and meron in fleas, while in the Coleoptera there is no such division of the mesothoracic coxa, and the Coleoptera therefore could not serve as the precursors of the fleas. Fleas apparently have cerci, whereas no known Coleoptera have cerci, so that on this basis also, the Coleoptera could not serve as the types ancestral to the fleas. On the other hand, it was pointed out in the publication cited above, that the Trichoptera could readily serve as the types ancestral to fleas since they have three-segmented labial palpi, their prothoracic sclerites are as much like those of the fleas as any insects, the mesothoracic and metathoracic coxæ of Trichoptera are divided into a eucoxa and meron, and the Trichoptera have cerci and terminal structures suggestive of those of the fleas.

The evidence furnished by a study of the metathoracic structures of fleas is so overwhelmingly convincing and may be so readily seen and appreciated by any one who is willing to give it a moment's attention, that it is indeed astonishing that no one has been willing to consider these structures in attempting to determine the affinities of the Siphonaptera. Any one who will

examine a common dog flea (Fig. 1) can readily see that its mesothorax and metathorax are subequal, while in any dipteran (Fig. 13) the metathorax is only a fraction of the size of the immensely developed mesothorax. Unless we completely reject Dollo's law of the irreversibility of evolution, we must assume that the ancestors of the fleas likewise had a mesothorax and metathorax subequal in size, and this would utterly preclude deriving fleas from Diptera, all of which (including the Phorids) have the metathorax reduced to a mere fraction of the size of the mesothorax. All of the fleas which I have examined have a metathoracic coxa divided into a eucoxa, or anterior region *ec* of Fig. 1 and a meron, or posterior region *me* of Fig. 1 and this is apparently typical of fleas in general, so that it was evidently a prominent feature in their ancestors. No known Diptera (not even phorids, etc.), however, have a well-developed meron in the posterior leg (see Figs. 9, 12, 13, 14, etc.), and such Mecoptera as *Boreus* shown in Fig. 6 (considered by Tillyard to represent a type ancestral to the Siphonaptera) likewise lack a well-developed meron in the metathoracic leg (although other Mecoptera have it quite well developed) so that the evidence from this source is in harmony with that furnished by the labial palpi and other structures indicating that the fleas could not be derived from the Diptera, or from such Mecoptera as *Boreus*.

When we compare the metathoracic structures of a typical flea such as the one shown in Fig. 1, with those of a parasitic coleopteron such as *Platypsylla*, shown in Fig. 3 (supposedly representing a type ancestral to the fleas, according to those who maintain that fleas were descended from coleopterous forebears or with the structures of any other Coleoptera, such as the ones shown in Figs. 26, 27, 34, etc., it is at once apparent that the suture between the episternum (*es*) and epimeron (*em*) is vertical in the flea, while in the Coleoptera under consideration, the metathoracic pleural suture (i.e., the suture between the episternum and epimeron) is more nearly horizontal. The ancestors of the fleas must have had a more nearly vertical pleural suture in the metathoracic region, and this would exclude from consideration such forms as the Hymenoptera and Coleoptera (which have a more oblique metapleural suture) in attempting

to determine the character of the ancestors of the Siphonaptera. Furthermore, the Hymenoptera and Coleoptera do not have a well-developed meron in the mesothorax, as the fleas do, and in the metathorax also, the meron is not typically developed in the Coleoptera and Hymenoptera (see Figs. 26, 27, 34, 18, 21, 22, etc.) while it is characteristic of fleas to have a well developed meron (*me* of Fig. 1) in the metathoracic leg, and the same must have been characteristic of their ancestors. Furthermore, the line of union between the metathoracic trochanter and femur tends to extend obliquely downward in the Coleoptera (Figs. 3 and 27) while in the fleas, the line of union between the trochanter and femur is not of this type—in fact the line of union is more “transeverse” or may even tend to slant in the other direction (i.e., “upward”) in the fleas. The metathorax is usually much larger than the mesothorax in the Coleoptera, while in the fleas, and probably in their ancestors also, the mesothorax tends to be of approximately the same size as the metathorax. In the Coleoptera the meso- and metathoracic sternal regions do not become narrowed and extend posteriorly between the legs and give off lateral extensions furnishing secondary points of articulation along the mesal surface of the legs, while in the fleas and probably also in their ancestors, the sternal region becomes extremely narrow between the legs and a lateral “wing” or extension of the sternal region (like that present in Trichoptera, etc.), is produced along the mesal surface of the leg (such an extension is shown in the mesothoracic region of the flea shown in Fig. 1—i.e., the structure labelled *le* in Fig. 1). All of these facts are in harmony with the conclusions reached from the study of other structures as well (e.g., the character of the terminal abdominal structures) indicating that fleas could not be derived from the Coleoptera, and for essentially the same reasons, the fleas could not be derived from the Hymenoptera either.

Since the evidence afforded by the structures thus far studied eliminates the Diptera, Coleoptera (with the Strepsiptera), Hymenoptera and such Mecoptera as *Boreus* from consideration as possible ancestors of the Siphonaptera, this leaves only the Trichoptera, Lepidoptera, Neuroptera and certain Mecoptera to

be considered in this connection (the character of the larval fleas indicates that the group is a Holometabolous one, and their ancestors must therefore have been Holometabola of some sort) and greatly simplifies the problem of determining the probable ancestors of the fleas.

The metathoracic meron *me* of the flea shown in Fig. 1 is rather suggestive of that of the lepidopteron shown in Fig. 2, and the metathoracic pleural suture *ps* is more vertical in both of these insects. The lepidopteron shown in Fig. 2, however, belongs to an order descended from Trichoptera-like forebears, and such resemblances as these might be due to the fact that both the fleas and Lepidoptera were descended from Trichoptera-like forebears. Furthermore, the Trichoptera are closely related to the mecopteroid forebears of the Diptera, and are the intermediate forms combining in themselves not only lepidopterous characters, but also many features occurring in the Mecoptera and their dipterous descendants, and any resemblances between the fleas and the Lepidoptera, on the one hand, or between the fleas and the dipterous descendants of the Mecoptera on the other, could be readily explained by their common relationship to the Trichoptera, which are intermediate forms related to the Lepidoptera and also to the Mecoptera and Diptera.

So far as their larvæ are concerned, fleas resemble the Diptera in many respects, especially in their legless condition, and in the development of their setæ; but in the structural details of the head capsule and mouthparts which are practically the only structures in larval fleas sufficiently well developed for comparison with other insects, the resemblance of flea larvæ to the larvæ of Trichoptera is even more marked, and such resemblances as are to be found in dipterous and siphonapterous larvæ may possibly be explained as the results of their mutual relationship to the Trichoptera. In fact, as I have pointed out on page 241 of the Brooklyn Entomological Society, Vol. XXV, for 1930, a study of the structural details of such primitive dipterous larvæ as those of the Tanyderidæ and Bibionidæ very clearly, indicates that the larvæ of the ancestral Diptera were like those of the Trichoptera as well as the Mecoptera, since these primitive dipterous larvæ resemble trichopterous larvæ quite as much as they

do the larvæ of the Mecoptera in their structural details, and since both Diptera and Siphonaptera resemble the Trichoptera in their larval stages, it is not surprising that larval Diptera and Siphonaptera resemble each other as well.

The larvæ of the higher Neuroptera such as the Planipennia, typically have the mandibles, etc., extremely elongated and sickle-shaped, and are quite unlike flea larvæ in this respect, while the larvæ of the lower Neuroptera have well developed thoracic legs and primitive head structures altogether different from those of flea larvæ, and the adult structures are likewise quite different from those of typical fleas, so that it is not very probable that fleas were derived from such primitive forms as the Neuroptera themselves, and the Mecoptera (ancestral to the Diptera) and the Trichoptera, with their offshoots, the Lepidoptera, furnish more promising material for attempting to reconstruct the types ancestral to the Siphonaptera.

As far as the meso- and metathoracic structures are concerned, adult Mecoptera could serve quite as well as the Trichoptera as the types ancestral to the fleas; but, as I have pointed out elsewhere (Crampton, 1925), the character of the labium of a typical flea, with its three-segmented labial palpi, distinct, well sclerotized submentum, etc., precludes our deriving fleas from Mecoptera, all of which have a labium with but two segments in the palpi, and the labium of all Mecoptera lacks the submental plate, etc., so that on this account we must seek for the ancestors of the fleas in some other type of Holometabola. This, then, leaves only the Lepidoptera and Trichoptera among the forms not excluded by some important anatomical features from serving as the prototypes of the Siphonaptera.

The Lepidoptera furnish extremely promising material for reconstructing the types ancestral to the Siphonaptera in so far as the anatomical characters of the adults are concerned, and the Lepidoptera include forms exhibiting a tendency toward parasitism (e.g., *Cryptoses* parasitic on the sloth) and their larvæ are terrestrial instead of being aquatic as the typical trichopterous larvæ are—although some trichopterous larvæ live in moss, etc., suggestive of a common habitat for the primitive Lepidoptera (micropterygids) and Trichoptera. The maxillæ,

prothoracic sclerites and terminal abdominal structures of adult fleas, however, point more nearly to a trichopteroid ancestry for the Siphonaptera (see Crampton, 1923, 1926 and 1929), and the head structures of larval fleas are so much more like those of trichopterous larvæ, that I am more inclined to consider that both fleas and Lepidoptera were descended from trichopteroid forebears having many things in common with these two derived groups, and the resemblances between the Siphonaptera and Lepidoptera would therefore be due to their mutual relationship to the Trichoptera. In deriving fleas from such a trichopteroid ancestry, I would not minimize the evident resemblances between the fleas and the Diptera, Mecoptera, Neuroptera, Trichoptera and Lepidoptera, and if the lines of descent of these forms were portrayed graphically, they should be shown as a "bush-like" figure drawn as though branching in three planes, instead of being depicted as a dichotomously branching tree drawn in one plane. The complicated interrelationships of these insects can be more readily understood after each group has been compared with its nearest relatives in the general scheme of the holometabolous orders.

There is practically no dispute among recent investigators regarding the ancestry of the Diptera, which are apparently descended directly from the Mecoptera, or from Mecopteroid ancestors by way of the fossil Paratrachoptera (Protodiptera) such as *Aristopsyche*—which may be a true mecopteroid, rather than a "paratrachopteron." The maxillæ (Crampton, 1932), the neck and prothoracic sclerites (Crampton, 1926), the terminal abdominal structures of the females (Crampton, 1929) and the male genitalia (Crampton, 1924, and 1931) are so similar in the two groups, that there can be no doubt whatsoever that the Mecoptera have preserved the ancestral features of the precursors of the Diptera in practically all of their structures in the adult condition—although the larval structures indicate that the Trichoptera as well as the Mecoptera are like the ancestors of the Diptera in many respects (Crampton, 1930). I have pointed out the resemblances between the mesothoracic terga of the Diptera and those of the Mecoptera (Crampton, 1919) and also called attention to the fact that such Neuroptera as the

Nemopteridæ foreshadow the modifications met with in the mesonota of the tipulid Diptera and the bittacid Mecoptera; and in the present paper I would call attention to the resemblances between the metathoracic and basal abdominal structures of the Diptera and Mecoptera, and the features in which these regions of the nemopterid neuropteran *Croce* foreshadow the conditions met with in the Diptera and bittacid Mecoptera.

The modifications occurring in the basal abdominal region of the bittacid mecopteran *Harpobittacus* shown in Fig. 16 are very like those exhibited by the ptychopterid dipteran *Bittacomorpha* shown in Fig. 13 in the slender character of this region of the abdomen, although the basal region of the more primitive dipteran *Protoplasa* shown in Fig. 9 is more like that of a primitive Mecopteron (Fig. 11) or even a primitive Neuropteran (Fig. 29). The metanotum *mn* in the Diptera shown in Figs. 9, 13 and 14 is greatly reduced, and the metathoracic pleural region is naturally much smaller than the mesothoracic pleural region due to the great reduction of the metathorax in all Diptera. An "adumbration" of the reduction of the metathorax of the Diptera is "foreshadowed" in the nemopterid neuropteran *Croce* shown in Fig. 10, in which the metathorax becomes markedly reduced, and the mesothoracic postscutellum *psl* is hugely enlarged (for a neuropteran) as the metanotum shrinks away from it, thus foreshadowing the condition exhibited in the Diptera more pronouncedly than is the case with these structures in the Mecoptera. Furthermore, the metathoracic coxa *cx*₃ of *Croce* (Fig. 10) has practically lost the meron present in lower Neuroptera (*me* of Fig. 29), although in certain Mecoptera such as *Boreus* (Fig. 6) the meron of the metathoracic leg is practically lost thus approaching the condition met with in the metathoracic leg of the Diptera (Figs. 9, 13, 14, etc.) in which the meron has completely disappeared. The venation of the hind wing of *Croce* (Fig. 10) suggests the beginning of the reduction of the hind wings to form the halteres of primitive Diptera which preserve traces of the venation in some Tipulids, etc., and the basal abdominal segments of *Croce* (Fig. 10) are very like those of certain tipulid diptera. The mouthparts of *Croce* and several other features suggest that the nemopterid

Neuroptera furnish the starting-point of the modifications met with in the Mecoptera and Diptera, but this does not mean that the nemopterid Neuroptera were the actual ancestors of either Mecoptera or Diptera. It does indicate, however, that in the original ancestral neuropteran stock there were developmental tendencies which would make themselves manifest in the derived mecopteran and dipteran groups, if given an opportunity for expression (by the proper combination of genes, etc.), and the condition exhibited by such Nemopterid Neuroptera as *Croce* may thus be regarded as adumbrations of the conditions later occurring in the Mecoptera and Diptera. This view is more probable than that both Diptera and Mecoptera were derived more or less independently from Neuropterous ancestors, since the Mecoptera (or mecopteroids) were evidently ancestral to the Diptera, although the Mecoptera themselves were apparently derived from primitive Neuroptera, which exhibited some features suggestive of the Diptera.

The Mecopterite *Nannochorista* shown in Fig. 7 has lost the sternite corresponding to the first abdominal tergite, so that in this respect, it is less primitive than the Dipterite *Protoplasma* shown in Fig. 9. The primitive trichopterite *Philopotamus* (Fig. 5) and the primitive Lepidoptera such as *Mnemonica* or *Micropteryx* (Fig. 4) which are extremely like *Philopotamus* in most of their structures (Crampton, 1920) both resemble *Nannochorista* (Fig. 7) very strikingly in the character of their basal abdominal and metathoracic structures (particularly in the character of the epimeron *em* and its connection with the post scutellum *psl*) and these representatives of the Lepidoptera, Trichoptera and Mecoptera shown in Figs. 5, 4, and 7, furnish an excellent series of forms leading from the Lepidoptera to the Trichopterous and higher mecopterous types, and from these to the lower mecopterous types (Fig. 11) leading to the primitive Neuroptera (Fig. 29). The color of these insects suggests that a very dark brown (or black) hue was characteristic of the series of insects leading from the Neuroptera to the Mecoptera (with the Diptera) and from these to the Trichoptera and Lepidoptera, instead of the yellowish brown which I formerly considered to be the color of the ancestors of these orders of insects. *Notio-*

thauma, which is the most primitive living representative of the Mecoptera is of a castaneous hue, and is more like the ancestral Mecoptera than is the pale brown *Merope*, which I formerly supposed was the most primitive representative of the Mecoptera, and this adds weight to the view that the ancestral Mecopteroids (from which the Diptera, Trichoptera, etc., were descended) were probably of a dark brown hue. The primitive Neuropteroid *Sialis* is also dark brown in color, and it is more probable that the insects in the line of descent of the neuropteroids or mecopteroids (i.e., Neuroptera, Mecoptera, Diptera, Trichoptera, Lepidoptera, etc.) were originally dark brown in color.

In attempting to determine what the ancestors of the primitive neuropteroids were like, the condition exhibited by such primitive Mecoptera as *Chorista* (Fig. 11) and such Neuroptera as *Chauliodes* (Fig. 29) is of interest. The metathoracic meron *me* is well developed in these insects, and their ancestors must have had a well developed meron also. This feature would point to an isopteroid ancestral type resembling the termite shown in Fig. 28, in which the meron *me* is extremely well developed. Roaches, however, such as the one shown in Fig. 33, also have a fairly well developed meron *me*, and the roaches as well as the termites are like the protorthopteroid (or protoblattoid) ancestors of the Holometabola—and the dark brown color typical of many roaches and termites may have some significance in this connection. The roaches and termites, however, do not have a well developed postscutellum, typically present in Neuroptera, Mecoptera and other primitive Holometabola, and on this account such orthopteroid insects as the embiids and Plecoptera, in which the postscutellum is well developed (see description by Crampton, 1918), should be taken into consideration in attempting to reconstruct the types ancestral to the Holometabola, since the roaches and termites lack the postscutellum characteristic of the neuropteroid Holometabola.

The Psocid *Zorotypus* (placed in the Psocoptera for reasons given in the paper by Crampton, 1922) presents a condition intermediate between the neuropteroid Holometabola (and the Hymenoptera also) and the Isoptera, and serves to connect the

two groups of insects quite well. *Zorotypus* (Fig. 31) has a postscutellum *psl* like that of the neuropteroid Holometabola (Figs. 11, 29, 7, etc., *psl*), while the ventro-lateral region of the pleuron of *Zorotypus* (Fig. 31) is like that of a typical termite, such as the one shown in Fig. 28, in having a laterosternal sclerite *ls* well developed and clearly demarked—although such primitive Orthopteroids as *Grylloblatta* (Fig. 8) also have a well developed laterosternite *ls* and might be considered as somewhat annectant between the Isoptera and the lower Holometabola such as the Coleoptera, etc. Despite the fact that it has no metathoracic meron, however, the psocid *Zorotypus* (Fig. 31) is the best intermediate form I know of for connecting the lower Holometabola in general with the Isoptera-like forebears of the Holometabola, and the psocid group to which *Zorotypus* belongs also exhibits features in common with the embiids and other orthopteroids having a well developed postscutellum. In this connection, it may be mentioned that although it is frequently stated that the postscutellum is vestigial or wanting in the Orthoptera, I have found the largest postscutellum that I have ever encountered in any insect except the Strepsiptera (Fig. 25) in the orthopteron *Rhipipteryx* shown in Fig. 15, and many of the “bush-crickets,” etc., have well developed postscutella, so that it is erroneous to suppose that the Orthoptera exhibit no tendency toward the development of a postscutellum.

In stating the *Zorotypus* is intermediate between the neuropteroid Holometabola and the Isoptera, and that the psocid group to which *Zorotypus* belongs also exhibits affinities with the embiids, I would emphasize the fact that it is necessary to use a “three-dimensional” figure to express the complicated interrelationships of the different insectan orders in a satisfactory manner. Furthermore, in reconstructing the types ancestral to the Holometabola, we have to take into consideration not only the blattids and Isoptera, but also the embiids and Plecoptera, and certain other orthopteoids such as *Grylloblatta* and the Dermaptera as well, since some of these forms have retained ancestral features which others have lost, and in reconstructing the archetypal form from which the Holometabola were derived, we must combine the ancestral features from all of these primi-

tive orthopteroids, since no one of them has retained all of the ancestral features which we know must have occurred in the precursors of the Holometabola (judging by the character of the structures exhibited by the most primitive representatives of the Holometabola). When such an archetype had been constructed by combining ancestral features from these orthopteroids, I think that it would be extremely like the psocid *Zorotypus* in many respects (although it would probably have a well developed meron, which is lacking in *Zorotypus* and its venation would be much more primitive than that of *Zorotypus*) and on this account, I have maintained that *Zorotypus* is anatomically intermediate between the Holometabola and the orthopteroid types ancestral to the Holometabola, without implying that the Holometabola were descended from *Zorotypus* or any other psocid, for that matter. The ancestral features preserved by *Zorotypus*, however, indicate that it is closely related to the actual ancestors of the Holometabola, and its evident relationship to the Isoptera would indicate that the Isoptera are very like the forms giving rise to both psocids (*Zoraptera*) and Holometabola; but the Isoptera are not the ancestors of the Holometabola either, since the actual ancestors of the Holometabola were apparently forms in the common protorthopteron-protoblattid stem which exhibited features now retained in many orthopteroid insects such as the blattids, Isoptera, grylloblattids, Dermaptera, embiids and Plecoptera. So far as the posterior metathoracic and basal abdominal structures are concerned, I think that the Isoptera (Figs. 28 and 30) have retained most of the ancestral features exhibited by these "stem forms" in the pleural and basal abdominal regions, and in the basal region of the leg, with its well developed meron, but in the tergal region, the embiids and Plecoptera have retained the postscutellum which the Isoptera and blattids have lost, so that in this region the *Zoraptera*, represented by *Zorotypus*, which have retained a condition intermediate between the Holometabola and the ancestral orthopteroid group, are more like the embiids and Plecoptera than they are like the Isoptera and blattids, while in the pleural region and the basal abdominal region, the *Zoraptera* are more like the Isoptera. In the basal region of the leg, however,

the Zoraptera are too specialized to be intermediate between the lower Holometabola and the ancestral orthopteroids, since the Zoraptera have lost the meral sclerite which was doubtless present in the ancestral orthopteroids as well as in the lower Holometabola (or at least in the neuropteroid Holometabola).

The larval stages of the Strepsiptera are very like those of the meloid and rhipiphorid beetles, so that it is very disappointing to find that the posterior metathoracic and basal abdominal regions of a typical strepsipteron such as the one shown in Fig. 25, are not very like these regions in a typical rhipiphorid, such as the one shown in Fig. 27. The metathoracic coxa of the strepsipteron (Fig. 25) tends to unite with the pleural region, and the pleural sclerites are so peculiarly specialized in the Strepsiptera, that they furnish no serviceable clews for determining the types ancestral to the Strepsiptera. The metathoracic postscutellum (*psl* of Fig. 25) is hugely developed in the Strepsiptera, so that it is reasonable to suppose that the types ancestral to the Strepsiptera must have exhibited a marked tendency toward the enlargement of the metathoracic postscutellum, but the metathoracic postscutellum *psl* is quite small in the typical Rhipiphorid shown in Fig. 27, and the postscutellum is not greatly developed in any Coleoptera that I have been able to find, so that these structures do not furnish any serviceable clews for determining the ancestors of the Strepsiptera, and we must therefore depend upon the evidence of the larval characters for determining the closest affinities of the Strepsiptera. The evidence, such as it is, apparently points to a coleopteroid ancestry for the Strepsiptera, but I am more inclined to think that the Strepsiptera and Coleoptera were both descended from a common ancestry than to think that the Strepsiptera are the direct descendants of Rhipiphorids, or any other Coleoptera.

The Coleoptera are the most "orthopteroid" of all the Holometabola, and the Dermaptera are the orthopteroid forms which have retained the most features like those of the Coleoptera, although this does not imply that the Coleoptera were descended from the Dermaptera, but merely indicates that the Dermaptera have retained many characters present in the protorthopteroid ancestors of the Coleoptera and other Holometabola (i.e., the

forms in the common protorthopteron-protoblattid stem from from which the Holometabola were derived). I have already called attention to the strong resemblance between the maxillæ of the Coleoptera and those of the Dermaptera (Crampton, 1923), and to the striking resemblance between the tergal sclerites of the Coleoptera and those of the Dermaptera (Crampton, 1918), and when the basal abdominal structures and metathoracic pleural regions of the Coleoptera and Dermaptera shown in Figs. 32 and 34 are compared together, the resemblance is no less striking. The Dermapteron *Apachys* shown in Fig. 32 has an extremely large spiracle *sp* thus exhibiting a tendency for the first abdominal spiracle to become very large—a tendency which has been carried to the extreme in the lymexylonid coleopteron shown in Fig. 34, and the metathoracic epimeron and episternum *em* and *es* of *Apachys* (Fig. 32) are greatly elongated and assume a “horizontal” position as is the case in the lymexylonid (or lymexylid) beetle shown in Fig. 34. On the other hand, the character of the basal abdominal and metathoracic regions of the primitive Lycid beetle shown in Fig. 26 is very suggestive of the condition exhibited by the blattid shown in Fig. 33, in many respects, and both blattids and Dermaptera have evidently retained certain ancestral features suggestive of the precursors of the Coleoptera (and other Holometabola) from the actual ancestral forms in the common protoblattid-protorthopteron stem from which the Holometabola, including the Coleoptera, were derived. This view is in harmony with the fact that *Grylloblatta* and the Isoptera, as well as the blattids and Dermaptera, exhibit features suggestive of the ancestors of the Coleoptera, etc., and is much more probable than the view that the Coleoptera were descended from the Dermaptera alone.

The basal abdominal structures (with the spiracles borne in the sclerotized areas), the metathoracic postscutellum and metapleural sclerites of the lycid beetle shown in Fig. 26 are very suggestive of these structures in the primitive sawfly (Hymenopteron) shown in Fig. 24, and this resemblance lends weight to the view that the Hymenoptera and Coleoptera are quite closely related based upon resemblances in the venation of the two groups, as well as upon other features which the Coleoptera

(with the Strepsiptera) and Hymenoptera have in common—such as the absence of a meral region in the mesothoracic coxae, while all other Holometabola tend to preserve the meron in the mesothoracic leg. The basal abdominal and metathoracic sclerites of such sawflies as the ones shown in Figs. 23, 19, 21, etc., are likewise suggestive of those of the Dermaptera shown in Fig. 17, which is also in harmony with the fact that their relatives the Coleoptera likewise resemble the Dermaptera in these respects, but the regions in question in the Hymenoptera are very suggestive of those of the Isoptera (Figs. 28 and 30) as well, and in most respects the Isoptera are more like the ancestors of the Hymenoptera than the Dermaptera are. This is in harmony with the fact that the Zorapterous Psocids are related both to the Hymenoptera and to the Isoptera, being anatomically intermediate between the Hymenoptera and Isoptera in many respects. The Hymenoptera, however, were evidently descended from the forms in the common protorthopteron-protoblattid stem from which the rest of the Holometabola were derived, and whatever resemblances the Zoraptera and Isoptera exhibit with the Hymenoptera are due to the retention of ancestral features from the common orthopteroid stem from which they and the Hymenoptera also were derived.

While the absence of the mesothoracic meron in Hymenoptera and Coleoptera (with the Strepsiptera) and its presence in other Holometabola would indicate a closer relationship between the Hymenoptera and the Coleoptera (as is also indicated by the venation as well as the basal abdominal structures, the position of the spiracles and the metathoracic sclerites of primitive Coleoptera and Hymenoptera) the Hymenoptera are no less closely related to the Neuroptera and mecopteroid Holometabola as is shown by the *Chrysopa*-like head and the ocelli of many sawflies, and by the *Rhapidia*-like terminal abdominal structures of the sawflies *Xyela*, *Sirex*, etc., and by the Mecopteroid male genitalia, cerci, larval characters, etc., of primitive Hymenoptera. We may therefore consider that the Hymenoptera occupy a position intermediate between the Coleoptera on the one side, and the Neuroptera with the mecopteroid insects, on the other,

and their ancestors had much in common with the Zorapterous psocids and the Isoptera.

In attempting to find the hymenopterous type intermediate between the sawflies (Chalastogastra) and the stinging Hymenoptera (Clistogastra) a study of the basal abdominal region (which is one of the important features for separating the sawflies from the stinging Hymenoptera) would indicate that the usual view that the oryssids, such as the one shown in Fig. 19, exhibit tendencies leading to the stinging type of Hymenoptera is incorrect, since the Cephidæ, such as the one shown in Fig. 18, exhibit a striking tendency toward the formation of a deep constriction between the first and second abdominal segments, and this tendency, if carried still further, would result in the formation of a pronounced constriction between the first and second abdominal segments (accompanied by a narrowing and elongation of the second abdominal segment) exhibited by the sting-bearing Hymenopteron shown in Fig. 20. Even in the sting-bearing Hymenopteron shown in Fig. 20, the first abdominal tergite labelled 1^t is broadly joined to the thorax, so that the abdomen is as broadly joined to the thorax (metathorax) in the sting-bearing Hymenoptera as it is in the sawflies, and it is most inaccurate to speak of one group as having the abdomen broadly joined to the thorax and the other as having a constriction between the abdomen and thorax, since no Hymenoptera seem to have a deep constriction between the thorax and abdomen, the actual constriction being between the first and second abdominal segments—as the systematists have long known to be the case, although they have persisted in retaining the incorrect descriptive designations handed down from the time when it was supposed that the first abdominal tergite (propodeum) was in reality the metanotum, and the true second abdominal segment of stinging Hymenoptera was interpreted as the first abdominal segment, as has been pointed out by Packard, Brauer, and many other investigators.

The condition exhibited by the cephid sawfly shown in Fig. 18 suggests that the narrow anepisternal and anepimeral regions *aes* and *aem* (i.e., the upper regions of the episternum and epimeron) form the narrow upper metapleural region labelled

aes in the ichneumonid hymenopteron shown in Fig. 20, although the anepisternum forms a larger part of this upper metapleural region than the anepimeron does. The katepimeron *kem* or lower portion of the epimeron in Fig. 18 becomes very narrow in Fig. 20, while the katepisterum *kes* or lower portion of the episternum in Fig. 18 forms the greater portion of the metapleuron labelled *kes* in Fig. 20. The propodeum 1^t of Fig. 20 is formed by the first abdominal tergite, labelled 1^t in Fig. 18. The second abdominal tergite 2^t of Fig. 18 tends to become markedly constricted basally (anteriorly) and in Fig. 20 it has apparently extended downward (in the anterior region) crowding the second sternite 2^s backward in the process, and in such stinging Hymenoptera I think that most of the petiole is formed by the second abdominal tergite rather than by the union of the second sternite and tergite. The region labelled *tm* in Fig. 18 apparently corresponds to the region called the tergomarginale (or tergomarginal sclerite) in the roach, etc., and, in Fig. 20, this sclerite (*tm*) forms a structure of use in the movements of the abdomen.

Many recent investigators regard the siricids as the nearest living representatives of the ancestors of the lower Hymenoptera. The character of the metathoracic and basal abdominal structures of the siricids very clearly indicates that the siricids such as the one shown in Fig. 21 are like the ancestors of such sawflies as the xiphidriidid shown in Fig. 23 and the oryssid shown in Fig. 19 (which is too much like these other siricoids to be placed in a different suborder from them) but the siricids (Fig. 21) are not like the ancestors of such sawflies as the one shown in Fig. 22, since these sawflies apparently lead back to ancestors more closely resembling the "Lydid" sawfly *Cephaleia* shown in Fig. 24 and the Xyelidæ, and I think that the latter sawflies are much more primitive than the siricids. *Cephaleia* has many features suggestive of orthopteroid affinities, and its ancestors were apparently derived from Isoptera-like forebears in the common protoblattid-protorthopteron stem instead of being the descendants of the fossil insects called "Protohymenoptera" by Tillyard, since Carpenter, 1931, has recently shown that the so-called "Protohymenoptera" are in reality specialized

Megasecoptera having nothing to do with the ancestors of the Hymenoptera. In this connection it may be remarked that the interpretation of the venation of the fore wing of the Hymenoptera suggested by a comparison with the fore wing of a Psocid, as given in Figs. 66 and 65 of Plate 9 in Vol. LIV of the Canadian Entomologist for 1922, is more nearly correct than the new interpretation suggested by Tillyard whose conclusions are based upon a comparison of the Hymenoptera with the unrelated Megasecoptera, in which he has mistaken the lower surface of the wing for the upper one, and consequently has confused the concave and convex veins, as was pointed out by Carpenter, 1931, who obtained some excellently preserved specimens of the "Protohymenopterous" Megasecoptera from the Kansas Permian formations, and was able to determine the character of the body of these insects as well as their wings.

When the bodies of the so-called "Protohymenoptera" were studied, it was found that their body structures were typically those of Megasecoptera, and the superficial resemblance of their wings to those of the Hymenoptera was found to be merely the result of convergence. This instance very clearly illustrates the inadvisability of basing one's conclusions on one set of structures alone. It is so easy to say that the disembodied wings of some fossil insect are ancestral to some modern group of insects, that there is a great temptation to claim to have found the actual ancestors of a modern group whenever one discovers some fossil wings that resemble those of any modern group, without waiting to discover what the body of the insect which originally bore the fossil wings was like, in order to determine if the ancestral relationship claimed for the fossil wings could be substantiated. The phenomenon of "heterospecialization" or unequal specialization in the different parts of the body of any one insect should make us very hesitant about accepting such claims based upon the study of the wings alone, since, as in the case of the so-called "Protohymenoptera," a study of the body might wholly overthrow the theory of an ancestral relationship based upon the study of the wings alone, and until something is known about the body of the insect which bore them, we cannot justly claim an ancestral relationship for any insect whose wings alone are

known. If it is found, however, that the relationships indicated by the wings are borne out by the study of other parts of the body, using for this purpose archetypes made by selecting the primitive features exhibited by the lowest representatives of each group of insects (or by the annectant types serving to connect several groups of insects) one can be much more confident that his conclusions are correct. Most of the recent students of insect phylogeny, however, are unwilling to make such studies themselves, and are not even willing to consider the evidence presented by others who have made such studies, with the result that it is impossible to find a reference in the text or bibliographies of most palaeoentomological papers to any studies of structures other than the wings, and the same is true of all recent text-books and so-called reviews of recent advances in entomology, with the result that beginning students and investigators alike are as completely ignorant of any evidence of relationships of insects, other than that furnished by the wings, as though such evidence did not exist. This attitude of utterly ignoring the easily accessible evidence already available for checking one's conclusions based upon one set of structures alone, is hardly in keeping with the modern scientific spirit; and when the students of wing-veins alone are at length willing to give enough consideration to the evidence of other structures as well (for understanding the interrelationships of insects) to be able to appreciate their value for checking the evidence from other sources, the study of various structures from widely different parts of the body will receive the consideration that it deserves instead of being completely ignored as is the case at present!

Since the evidence of the mouthparts, neck and prothoracic sclerites and terminal abdominal structures of female insects clearly supports the evidence of the wing-veins indicating that the blattids (with the protoblattids) Mantids and Isoptera form a compact superorder of insects (the Panisoptera) representing more closely than any others the protoblattoid ancestors of the Neopterygota, or higher insects capable of laying the wings back along the abdomen in repose (i.e. the orthopteroids, hemipteroids, psocoids and Holometabola), we may safely conclude that all of these Neopterygota were ultimately descended from

protoblattoid ancestors in the common protoblattid-protorthopteran ancestral stem.

The evidence of the head capsule, thoracic sclerites and terminal abdominal structures points to the psocoids (including the Zoraptera) and to some extent to the Homoptera, as the intermediate types connecting the Holometabola with the ancestral protoblattoids in the common protoblattid-protorthopteran stem; but the wing-veins of the Zoraptera, for example, are too specialized to serve as connecting links, as many of the body structures do in the Zoraptera, so that in this case the venational archetypes must be reconstructed from other sources, and, of living insects, the blattoid insects have retained more venational features suggestive of the ancestors of the Holometabola than any other recent forms have. In fact, I consider that the common ancestor of the holometabolous insects was more nearly a protoblattid than anything else (judging from the venational evidence), although it evidently exhibited many protorthopteran features as well.

The Holometabola as a group exhibit too many characters in common (especially in their larval stages) to be of a polyphyletic origin. The Coleoptera (with the lampyroids and silphids as their most primitive representatives) are the most orthopteroïd of the Holometabola in their general body structures, but the Neuroptera have retained a more primitive venation than the Coleoptera, and have also remained more primitive in their general body structures than have the Mecoptera, which have also retained a very primitive venation. The Coleoptera are more like the Neuroptera in their larval stages, but in the general character of the structures of the body, they are more closely allied to the Hymenoptera, which exhibit characters annectant between the Coleoptera, on the one side, and the Neuroptera and Mecoptera on the other. We are thus obliged to consider the venational evidence furnished by the Neuroptera and their allies the Mecoptera in determining their probable ancestral types, but the general body characters of the adults (and larvæ) are of more value for determining the affinities of the Coleoptera—although so far as their relationship to the Hymenoptera is concerned, the venational evidence is of some value also.

The various body structures are in complete agreement with the venational evidence in pointing to a close relationship between the Neuroptera, Mecoptera, Diptera, Trichoptera and Lepidoptera, but the body structures in general would indicate that the Neuroptera are more primitive than the Mecoptera are, and would point to an extremely close relationship between the Mecoptera and the Diptera, and between the Trichoptera and the Lepidoptera, although the Trichoptera are evidently related to the Diptera, Mecoptera and Neuroptera as well.

Of the specialized parasitic orders, the Strepsiptera are evidently closely related to the rhipiphorid Coleoptera, as is indicated by their larval structures; but their relationship to the rhipiphorids is not indicated by many structures of the adults, unless we attach especial weight to such rather trivial structures as the antennæ, etc. The fleas, on the other hand, occupy a rather isolated position, and it is extremely difficult to determine their closest affinities. They undoubtedly exhibit certain larval features suggestive of affinities with the Diptera, but on the whole they present more features in common with the Trichoptera (and their relatives the Lepidoptera). The fleas are likewise related to the Mecoptera and the Neuroptera; but their relationship to the Coleoptera is much more distant, and they have but slight affinities with the Hymenoptera.

In order to express all these interrelationships, we may divide the Holometabola into three superorders. The first superorder, or *Pansiphonaptera*, includes the Siphonaptera (fleas) alone, and represents a rather isolated group (related to the Trichoptera, Lepidoptera, Diptera, Mecoptera and Neuroptera) characterized as follows. They are laterally compressed apterous forms, with piercing mouthparts in which the labial palpi are composed of at least three segments, and the submental sclerite is usually distinct and well sclerotized. The mesothorax and metathorax are subequal. The pleural suture tends to remain more vertical, and the meron is frequently demarked in the meso- and metathorax. The abdominal spiracles are borne in sclerotized areas and what appear to be cerci are present in the terminal abdominal region of many fleas. They might be included

in the next superorder, but are hardly to be included with the Coleoptera.

The superorder *Panmecoptera* includes the Neuroptera, Mecoptera, Diptera, Lepidoptera and Trichoptera, with their fossil allies (such as Belmontia, Aristopsyche, etc.) and may be characterized as follows. Typically winged forms in which there is a tendency to suppress the anal region of the hind wings although certain Trichoptera do not exhibit this tendency very strongly. The body tends to be more robust than compressed. The mesothoracic leg typically exhibits a demarked meron. The metathorax is smaller than the mesothorax in some forms. The abdominal spiracles are typically borne in the lateral membranous region. The male genitalia are typically forcipate. The cerci are frequently developed. Within the superorder, the Mecoptera are very closely allied to the Diptera, and the Trichoptera are very closely allied to the Lepidoptera. The Neuroptera are allied to both Mecoptera and Trichoptera, though the line of development of the Trichoptera apparently joins that of the Mecoptera as they both lead back to neuropteroid forebears to which the Mecoptera are the more closely related.

The superorder *Pancoleoptera* includes the Coleoptera, Strepsiptera and Hymenoptera, with their fossil allies (but does *not* include the so-called "Prothymenoptera"). The body is more robust, and tends to become more depressed in some members of the group (certain Coleoptera). The hind wings sometimes retain a faint suggestion of traces of the anal fan of their orthopteroid ancestors. The mesothoracic legs never exhibit a demarked meron (thus differing from the members of the preceding superorder). The metathorax sometimes surpasses the mesothorax in size, and the metathoracic pleural suture frequently becomes more horizontal than vertical. The abdominal spiracles are usually surrounded by sclerotized areas, thus differing from the preceding superorder. Cercal and forcipate genitalia are developed only in the Hymenoptera, which are thus more like the Mecoptera than the Coleoptera are, and the larvæ of the Hymenoptera are more like those of the Mecoptera, Lepidoptera, etc., than the larvæ of the Coleoptera are, although the larvæ of certain Coleoptera are striking like those of certain

Neuroptera, and the wings of adult Coleoptera are more like those of the Neuroptera than is the case with the Hymenoptera. Although the Hymenoptera resemble the Mecoptera in many respects, and the Coleoptera resemble the Neuroptera in many respects, the Hymenoptera and Coleoptera (with their offshoots, the Strepsiptera) have been grouped in the same superorder because of their many similarities. When more is known of the fossil relatives of these insects, they might be placed in distinct superorders, but in the present state of our knowledge it is inadvisable to separate them further.

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ABBREVIATIONS

The subscripts 2 to 3 written after the labellings indicate that the structure designated by the label belongs to the mesothorax and metathorax respectively. The letters t and s written to the right and above the numerals denote the tergite and sternite of the abdominal segment indicated by the numerals.

aem	Anepimeron (upper region of epimeron)
aes	Anepisternum (upper region of episternum)
bs	Basisternum
ex	Coxa
ec	Eucoxa (anterior division of coxa)
em	Epimeron
es	Episternum
fe	Femur
fs	Furcasternum
h	Basal portion of halter
kem	Katepimeron (lower region of epimeron)
kes	Katepisternum
le	Lateral extension of furcasternum
ls	Laterosternite
m	Mediotergite (median region of postscutellum)
me	Meron
mn	Metanotum
ms	Mesonotum
p	Pleurotergite (lateral region of postscutellum) also called postalare
pes	Preepisternum

po	Posthaltere
pr	Prehaltere
ps	Pleural suture
psl	Postscutellum
sl	Scutellum
sp	Spiracle
st	Subtergite
tn	Trochantin
tm	Tergomarginale (marginal sclerite of tergite)
tr	Trochanter

PLATES

Unless otherwise stated, all figures represent lateral views of the posterior metathoracic and basal abdominal region of the insect's left side. The anterior region is directed toward the left hand margin and the dorsal region is directed toward the top of the plate. Wings and halteres are cut off, and the legs are cut off below the coxa in most cases.

PLATE XX

- Figure 1. Mesothorax, metathorax and basal abdominal region of the dog flea with mesothoracic coxa removed to show the lateral extension of the furcasternum *le* extending along its mesal face.
- Figure 2. Posterior metathoracic and basal abdominal region of the Lepidopteron *Danaus archippus*.
- Figure 3. Same of the coleopteron *Platypsylla*.
- Figure 4. Same of the lepidopteron *Eriocrania calthella*.
- Figure 5. Same of the trichopteron *Philopotanus*.
- Figure 6. Same of the mecopteron *Boreus*.
- Figure 7. Same of the mecopteron *Nannochorista dipteroides*.
- Figure 8. Same of the orthopteron *Grylloblatta campodeiformis*.

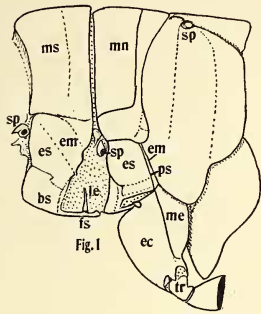


Fig. 1

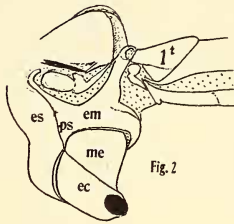


Fig. 2

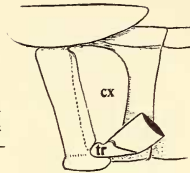


Fig. 3

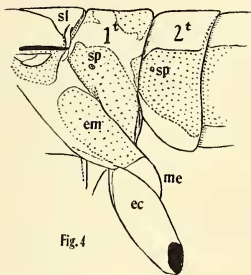


Fig. 4

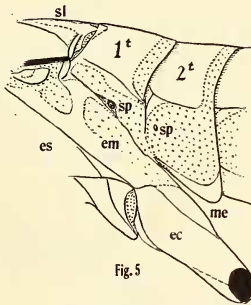


Fig. 5

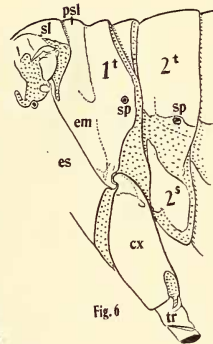


Fig. 6

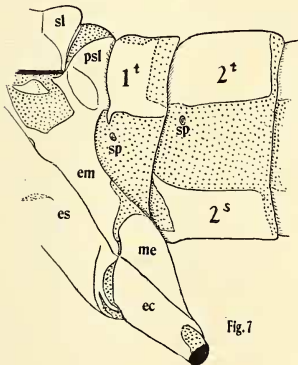


Fig. 7

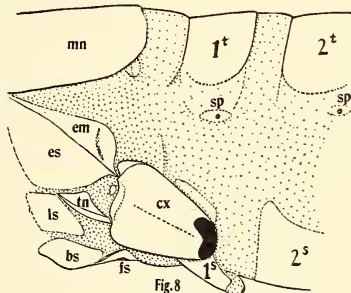


Fig. 8

PLATE XXI

- Figure 9. Posterior mesothoracic, lateral metathoracic and basal abdominal region of the tanyderid dipteran *Protoplasa fitchii*.
- Figure 10. Same of the nemopterid neuropteran *Croce filipennis*.
- Figure 11. Posterior metathoracic and basal abdominal region of the mecopteran *Chorista australis*.
- Figure 12. Posterior mesothoracic, lateral metathoracic and basal abdominal region of the dipteran *Leptis*.
- Figure 13. Same of the dipteran *Bittacomorpha clavipes*.
- Figure 14. Same of a mycetophilid dipteran *Sciara* sp. from Mexico.
- Figure 15. Posterior metathoracic and basal abdominal region of the orthopteran *Rhipteryx atrata*.
- Figure 16. Same of the mecopteran *Harpobittacus*.
- Figure 17. Same of the dermapteran *Arixenia*.

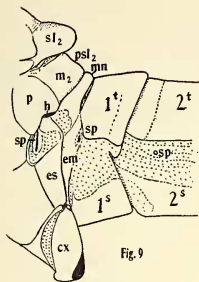


Fig. 9

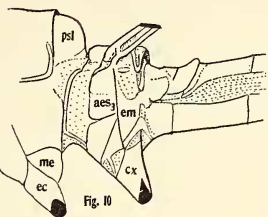


Fig. 10

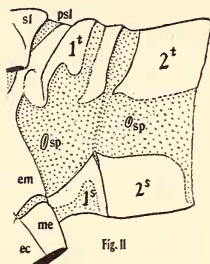


Fig. 11

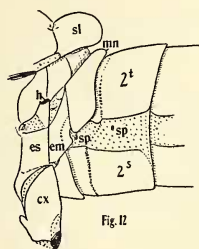


Fig. 12

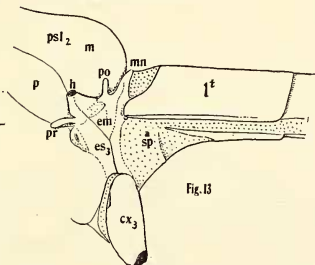


Fig. 13

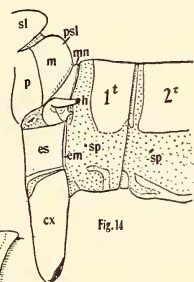


Fig. 14

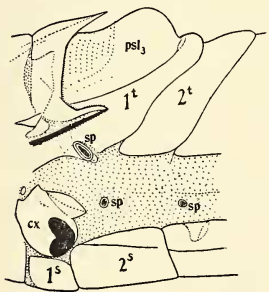


Fig. 15

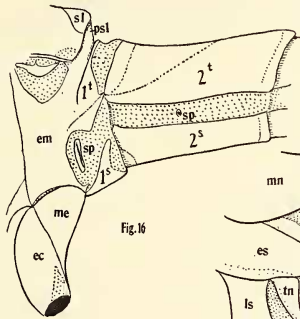


Fig. 16

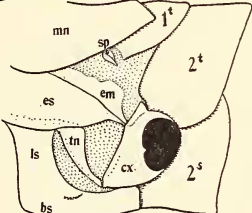


Fig. 17

PLATE XXII

Figure 18. Same of the cephid hymenopteron *Cephus* (Janus ?).

Figure 19. Same of hymenopteron *Oryssus*.

Figure 20. Same of ichneumonid hymenopteron *Megarhyssa*.

Figure 21. Same of hymenopteron *Sirex*.

Figure 22. Same of tenthredinid hymenopteron *Abia*.

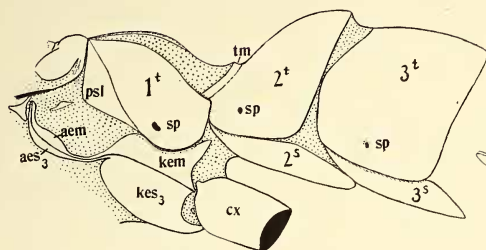


Fig. 18

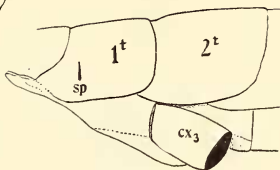


Fig. 19

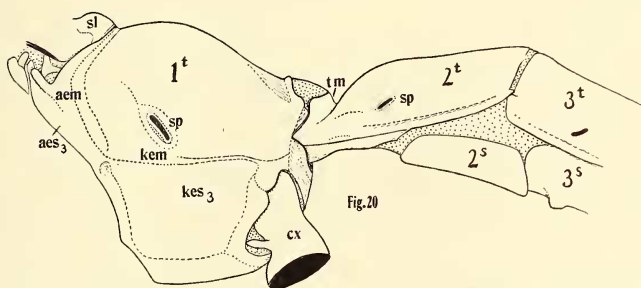


Fig. 20

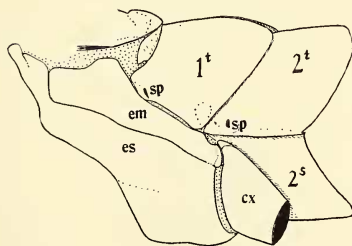


Fig. 21

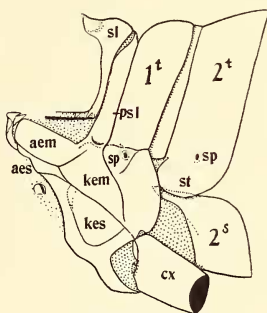


Fig. 22

PLATE XXIII

- Figure 23. Same of hymenopteron *Xiphidria*.
Figure 24. Same of lydid sawfly.
Figure 25. Same of strepsipteron (probably *Xenos*).
Figure 26. Same of lycid coleopteron.
Figure 27. Same of rhipiphorid coleopteron.

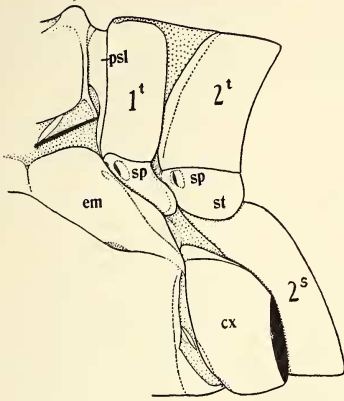


Fig. 24

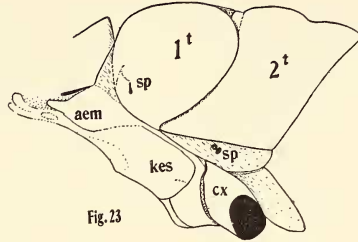


Fig. 23

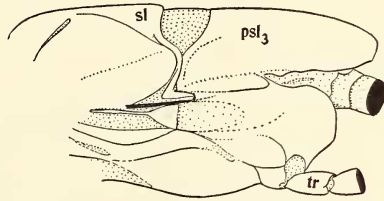


Fig. 25

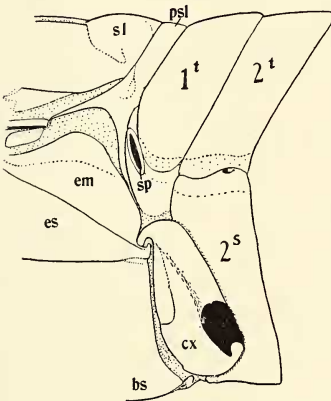


Fig. 26

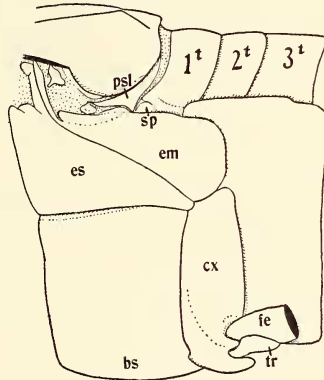


Fig. 27

PLATE XXIV

- Figure 28. Same of isopteron *Leucotermas flavipes* (alate caste).
Figure 29. Same of sialid neuropteran *Chauliodes*.
Figure 30. Same of termite *Termes bellicosus* (soldier caste).
Figure 31. Same of zorapterous psocid *Zorotypus snyderi*.
Figure 32. Same of dermapteron *Apachys*.
Figure 33. Same of roach *Periplaneta americana*.
Figure 34. Same of lymexylid (lymexylonid) coleopteron.

